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FRESHWATER TRICLADS (TURBELLARIA) OF
NORTH AMERICA. I. THE GENUS *PLANARIA*.¹

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The genus *Planaria* was established by O. F. Müller (1776: 221) to separate the free-living lower worms from the parasitic trematodes which retained the older name *Fasciola*. Originally *Planaria* comprised all known Turbellaria living in fresh water, in the sea, and on land and, besides these, the present Nemertina or Rhynchocoela. The extent of the genus was gradually narrowed as newly established genera were separated from it, chiefly by Dugès (1828), Ehrenberg (1831), and Örsted (1843 and 1844). After Ehrenberg's revision of the system, which first introduced the name Turbellaria, *Planaria* was restricted to turbellarians with branched intestine ("Dendrocoela") which possessed two eyes. Örsted, who further refined the systematic arrangement of the "flatworms," separated the polyclads ("Cryptocoela") from the Dendrocoela and applied the name *Planaria* mainly to triclads, both freshwater and marine, including also the many-eyed species which Ehrenberg had separated from *Planaria*. In 1844 (p. 51) he removed from it the new genus *Dendrocoelum* on the basis of its intestinal branching. In the following years the name *Planaria* was used rather indiscriminately for many turbellarian forms. With the progress of the studies of the internal structure of the various turbellarian taxa in the second half of the nineteenth century it gradually became restricted to freshwater triclads.

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Even today the common name "planarian" may signify any triclad species (freshwater, land, and sea planarians for Paludicola, Terricola, and Maricola).

It was not until the twentieth century that further important studies were reflected in the classification of the freshwater triclads. Thus Komárek (1926) proposed a more "natural" system of the Paludicola for the European representatives of this group. He established the genera *Dendroplanaria* (for Müller's *Fasciola torva*), *Fonticola*, and *Albiplanaria*, revived Hesse's (1897) *Euplanaria*, and restricted the generic name *Planaria* to Dana's (1766) *Hirudo alpina*.

The present system of the freshwater triclads, which is in principle being followed by modern authors, was introduced by Kenk (1930). The suborder Paludicola or Probursalia of the order Tricladida is divided into two families, the Planariidae and the Dendrocoelidae. A third family, Kenkiidae, split off from the Planariidae by Hyman (1937) appears not to be justified and has not been accepted by some later planarian workers (e.g., de Beauchamp, 1961: 103; Mitchell, 1968: 615-618).

The two families are distinguished by the arrangement of the muscle fibers in the internal muscular zone of the pharynx, which in the Planariidae consists of two distinct layers, a layer of circular fibers adjoining the internal epithelium, followed by a layer of longitudinal fibers; in the Dendrocoelidae the internal muscular zone is represented by a single layer of intermingled circular and longitudinal muscle fibers. Fortunately, this characteristic can be recognized even in sexually immature specimens, while many of the generic and specific features used in the identification of the smaller taxa concern primarily the reproductive system.

Komárek's (1926) restriction of the genus *Planaria* to *P. alpina* and its immediate relatives was untenable, since the species *alpina* was not included among the species assigned to the genus *Planaria* when it was first established by O. F. Müller (1776). Kenk (1930: 293) therefore selected *Fasciola torva* Müller (1774) as the type of the genus and presented a definition of the genus, slightly emended in a later paper (1935: 111): Planariidae whose oviducts—without embracing the

stalk of the bursa copulatrix (or forming a loop around it)—unite to a common oviduct which opens into the genital atrium. Male atrium without radial muscle plates. Adenodactyl present, constructed according to the *Planaria torva* type. (An analysis of the adenodactyl was given by Kenk, 1930: 159.)

In this narrower sense the genus *Planaria* comprises very few species, scattered over three continents: *P. torva* (Müller, 1774) with its probable synonym *P. onegensis* Zabusov (1901), in Europe and possibly Asia; *P. kempfi* Whitehouse (1913), in India; and *P. dactyligera* Kenk (1935), in North America.

A detailed review of the present status of the type species, *Planaria torva*, has been presented recently by Ball, Reynoldson and Warwick (1969).

Planaria dactyligera dactyligera Kenk, 1935

Type material: Holotype, from Mountain Lake, Giles County, Virginia, 2 slides of sagittal sections, U. S. National Museum No. 39461. Paratypes in the author's collection.

The species *Planaria dactyligera* has been described in detail in an earlier paper (Kenk, 1935: 105–110) from material collected in several localities in Virginia. Examination of specimens from North Carolina made it advisable to distinguish two subspecies of this species. The principal characteristics of the typical form from Virginia may be briefly recapitulated here.

External features: Mature animals are up to 13 mm long and 1.75 mm wide. The dorsal side is darkly pigmented, gray, brown, or black; the ventral surface, somewhat lighter. The anterior end is truncate, with almost straight frontal margin and rounded lateral (auricular) edges. In the quietly gliding animal there may be an insignificant narrowing or neck behind the auricles. Eyes are normally two, placed rather close together (about $\frac{1}{3}$ the width of the head at the level of the eyes) and removed from the frontal margin by a distance slightly less than the width of the head.

Reproductive system: The main features distinguishing the species from its relatives are in the anatomy of the reproductive system (cf. Kenk, 1935, figs. 25 and 27). The testes are predominantly ventral and occupy a pair of broad bands, one on either side of the midline, extending from a short distance behind the eyes to about the level of the mouth opening. The vasa deferentia expand in the region of the pharynx to form a pair of sinuous spermiducal vesicles (or false seminal vesicles), filled with sperm, as is typical for freshwater triclad in general. They approach the bulb of the penis from the antero-lateral sides. The two oviducts (or ovovitelline ducts), which in their main course accompany the

ventral nerve cords, turn upward and medially in the region of the copulatory complex and unite in the space above the male atrium and below the stalk of the copulatory bursa to form the common oviduct.

There is no distinct common genital atrium developed, as the various cavities of the copulatory organs meet in the immediate vicinity of the genital aperture: from the anterior side the male atrium, dorsally the duct of the copulatory bursa, and posteriorly the opening of the adenodactyl. The male atrium is more or less cone-shaped, duplicating the shape of the penis which it encloses.

The penis consists of a spherical bulb embedded in the mesenchyme and a conical papilla protruding into the male atrium. At the transition between the two parts is a cavity (the shape of which may vary according to the contraction or expansion of the organ), the seminal vesicle. This cavity receives from its anterior side the two vasa deferentia which have entered the bulb from the sides and have formed a few convolutions within the bulb, with a common opening. From the seminal vesicle the ejaculatory duct emerges as a tapering, straight canal which opens at the tip of the papilla. Many gland ducts penetrate the penis bulb from the surrounding mesenchyme and open into the seminal vesicle.

The muscular coat underlying the outer epithelium of the penis papilla consists of two layers: a circular layer adjoining the epithelium, followed by a layer of longitudinal fibers. The thickness of this muscle coat is about equal to, or slightly greater than, that of the wall of the male atrium.

The common oviduct formed by the union of the paired oviducts enters the posterior part of the male atrium from the dorsal side or from the left. The terminal parts of the paired oviducts and almost the entire common oviduct receive very numerous gland ducts filled with an intensely eosinophilic secretion.

The copulatory bursa is a large sac lying between the pharyngeal pouch and the bulb of the penis. Its duct or stalk, running dorsally to the male atrium, curves postero-ventrally and joins the atrial complex close to the gonopore. There is no distinct posterior portion or vagina developed.

The adenodactyl is a large hollow organ lying behind the genital aperture and opening close to the aperture without a prominent protruding papilla. Its heavy muscular wall is pierced by numerous gland outlets emptying its inner cavity.

Distribution: The type locality of *Planaria dactyligera dactyligera* is Mountain Lake, Giles County, Virginia, near south bank of the lake. It has been collected also in Rockbridge, Highland, and Albemarle counties, Virginia (Kenk, 1935: 109). Fite (1952), who studied a nematode parasitic in the pharynx of this species, collected his material at Twin Springs near the Mountain Lake Biological Station of the University of Virginia, in Giles County.

Chandler (1966: 11) reports that he collected some, mostly immature, planarians near Bloomington, Monroe County, Indiana, which he tentatively identified as *Planaria dactyligera*. He kindly sent me a slide of the

problematic species for examination. The preliminary identification proved to be erroneous.

***Planaria dactyligera musculosa* new subspecies³**

Type material: Holotype, from Ossipee, Alamance County, North Carolina, 4 slides of sagittal sections, U. S. National Museum No. 39462. Paratypes, 13 series of sagittal and transversal sections, in the author's collection.

External features: Mature specimens attain a length up to 11 mm and a width of 1.3 mm. The head is truncate, with the frontal margin slightly bulging in its entire extent (Fig. 1a) or in the central portion (Fig. 1b). In quiet gliding either of these two shapes may be assumed transitorily. The lateral edges are rounded. A very slight narrowing (neck) may be seen behind the head, then the body margins gradually diverge, remain parallel for some distance, converge again behind the pharyngeal region, and meet in the bluntly pointed posterior end. There are two eyes, lying close together (less than $\frac{1}{4}$ the width of the head at the level of the eyes) and farther distant from the frontal margin than from the lateral margins.

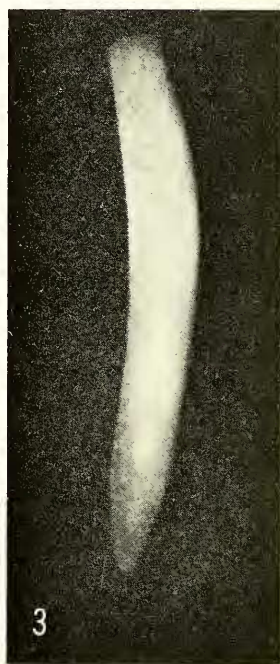
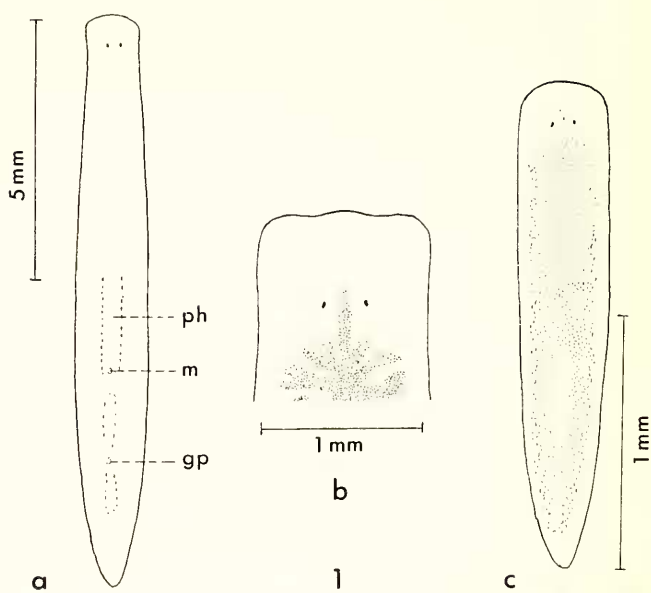
The pigmentation of the dorsal surface is usually dark, almost black, appearing somewhat cloudy under magnification. Only the two eye patches are free of pigment. There are, however, lighter areas visible above the pharynx and, in sexually mature specimens, above the copulatory complex. The ventral side is also pigmented, but in a lighter hue than the dorsal side. The mouth opening is visible as a distinct white spot, the gonopore is not quite as clearly discernible. Freshly hatched young are unpigmented, white, and acquire their pigmentation gradually during their growth and development. Animals kept in cultures in the dark tend to be more lightly pigmented than specimens in their natural habitat.

The pharynx is inserted at about the middle of the body, its length being approximately $\frac{1}{4}$ the body length. The mouth and the gonopore divide the posterior half of the body into three almost equal thirds.

As is seen from this description, *Planaria dactyligera musculosa* cannot be distinguished from *P. d. dactyligera* by its external features. It also resembles closely some pigmented species of *Phagocata* (*P. velata* [Stringer], *P. vernalis* Kenk, *P. crenophila* Carpenter, and at least one other, undescribed, species of this genus) as well as *Hymenella retenuova* Castle.

Internal characters: The anatomical characteristics of *Planaria dactyligera musculosa* conform in most particulars with those of the typical form (cf. Kenk, 1935: 105–109). The body pigmentation obscures the intestinal branching in the living specimens. The anterior end of the prepharyngeal intestinal ramus extends far into the head, forming a straight, unbranched diverticulum which reaches to a level anterior to the eyes (Fig. 1b).

³ *musculosus*, Latin, muscular, referring to the circular muscle layer of the penis papilla.



The testes are predominantly ventral, but individual follicles may be displaced dorsally or, at full maturity, may occupy the entire dorsoventral diameter of the body. The testicular zone of each side extends from a level behind the eyes to approximately the level of the mouth opening. The ovaries (with large parovaries), vitellaria, ovovitelline ducts, and vasa deferentia do not deviate from the conditions seen in the typical form. There are, however, distinct differences in the copulatory apparatus of the two subspecies.

A semidiagrammatic view of the copulatory apparatus of *Planaria dactyligera muscosa*, with particular reference to its muscular and glandular differentiations, is shown in Figure 4. In comparing this figure with the corresponding diagram for *P. dactyligera dactyligera* (Kenk, 1935, Fig. 27), the differences in the proportions of the individual organs should be disregarded, as the present figure is based on an unusually well extended specimen while that of the type-species shows a certain amount of longitudinal contraction such as is commonly encountered in preserved planarians.

In the new subspecies, the large copulatory bursa (*b*) regularly shows numerous lobes or diverticula projecting mainly in the lateral direction. The bursa duct (*bd*) gradually widens as it curves toward the gonopore, but shows no histologically distinct or sharply demarcated vagina. It opens into the atrial complex close to the gonopore (*gp*).

The penis consists of a spherical bulb containing loosely arranged muscle fibers running in more or less concentric layers, and the end parts of the sinuous and highly muscular vasa deferentia (*vd*). The bulb is pierced by numerous gland ducts which enter it from a wide area of the surrounding mesenchyme and open into the seminal vesicle (*vs*).

The two vasa deferentia empty, by a common opening, into the cavity of the penis which shows an anterior wider part (seminal vesicle, *vs*) and tapers posteriorly to a narrower ejaculatory duct which opens at the tip of the papilla. One of the chief distinguishing features of the new subspecies is the extraordinary development of the external circular muscle layer (*mp*) at the basis of the penis papilla. The thickness of this layer is several times the thickness of the muscle layers of the male atrium (while in *P. dactyligera dactyligera* the corresponding muscle layers are about equal in thickness).

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FIG. 1-3. 1. *Planaria dactyligera muscosa*. a. Quietly gliding animal; *gp*, gonopore; *m*, mouth; *ph*, pharynx. b. Anterior end, showing position of eyes and intestine. c. Freshly hatched young; the shaded area indicates the extent of the intestinal trunks and branches. 2. *Planaria dactyligera muscosa*, photograph from life, $\times 9$. 3. *Planaria occulta*, photograph from life, $\times 9$.

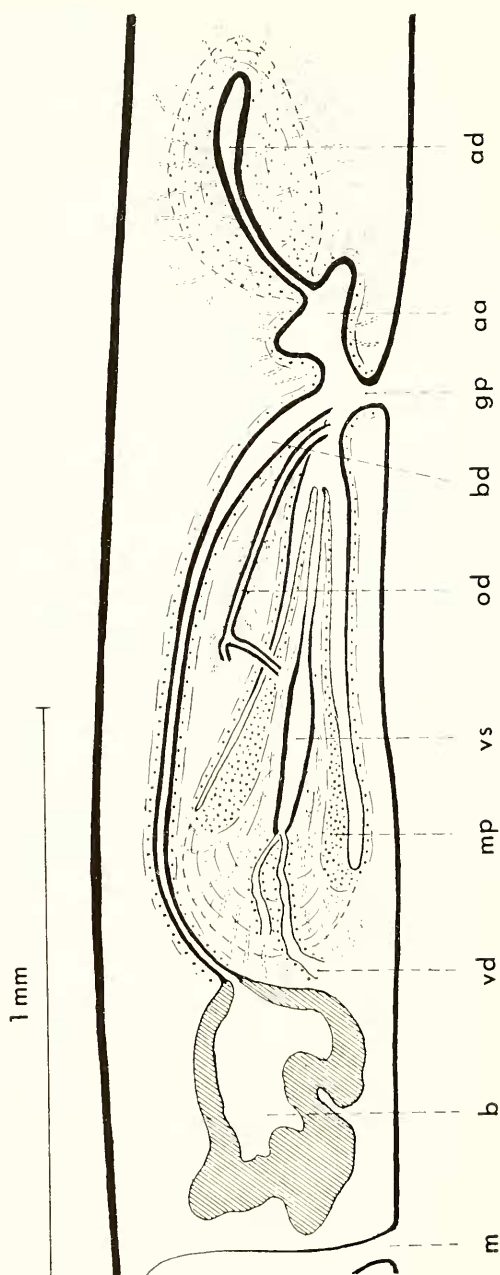


FIG. 4. *Planaria ductyligera musculosa*, semidiagrammatic view of copulatory organs in sagittal section. *aa*, atrium of adenodactyl; *ad*, adenodactyl; *b*, copulatory bursa; *bd*, bursa stalk; *gp*, gonopore; *m*, mouth; *mp*, circular muscle layer of penis papilla; *od*, common oviduct; *vd*, vas deferens; *vs*, seminal vesicle.

The second difference between the two forms concerns the relation of the adenodactyl (*ad*) to the atrial complex. The adenodactyl is a large ovoid or pear-shaped organ with a thick muscle coat of chiefly circular fibers, very densely arranged, with the corresponding cell nuclei forming a peripheral layer. Its elongated cavity opens into a separate part of the genital atrium (*aa*) which narrows anteriorly and connects with the general atrial complex very close to the genital opening (*gp*). There is no distinct papilla of the adenodactyl protruding into this chamber. The epithelium of the chamber is pierced by very many gland outlets originating in the mesenchyme.

In summary, the main distinguishing characteristics of the new subspecies are (1) the thick circular muscle layer at the base of the penis papilla and (2) the presence of a highly glandular antechamber between the gonopore and the adenodactyl.

Distribution: The first specimens of *Planaria dactyligera musculosa* were sent to me by Dr. T. E. Powell, Jr., of the Carolina Biological Supply Company. They had been collected at the "Sawdust Pile Location" in Ossipee, Alamance County, North Carolina, in November 1966. The majority of the animals were sexually mature.

Additional specimens were collected on 13 June 1968 in two localities on the grounds of the Warren Laboratories of the Carolina Biological Supply Company, off U. S. Highway 158, 3 miles E of Warrenton, Warren County, North Carolina. One was a stream near the side entrance road to the Laboratories, the other on the airport road. The specimens were small, immature, but matured in the laboratory cultures.

Reynierse and Ellis (1967) report that they used *Planaria dactyligera* in an experiment on planarian behavior. Since they had obtained their animals from the Carolina Biological Supply Company (personal communication), we may safely assume that their planarians belonged to the subspecies *P. d. musculosa*.

Longest (1966: 39-41) reported *Planaria dactyligera* from Abita Springs State Park, St. Tammany Parish, Louisiana. Examination of his slides showed that his specimens belonged to the subspecies *musculosa*.

Parasites: Small nematodes were occasionally observed in the mesenchymatous zone of the pharynx. They apparently were capable of moving freely through the tissue as no cysts were formed around them. The holotrichous ciliate, *Sieboldiellina planariorum* (Siebold) occurred in the lumen of the intestine and sometimes in the pharyngeal pouch. Some of the specimens were infested with the peritrichous ciliate epizoite, *Urceolaria mitra* (Siebold), attached mainly to their dorsal surfaces.

Observations in laboratory cultures: Cultures of *Planaria dactyligera musculosa* were kept in spring water in a constant-temperature chamber at about 14°C, and fed beef liver and/or *Tubifex* which were readily taken. The worms produced cocoons all year round. The cocoons are ellipsoidal, rather variable in size, the longest diameter measuring 0.8-1.7 mm, the shortest 0.6-1.0 mm. When deposited they are attached to

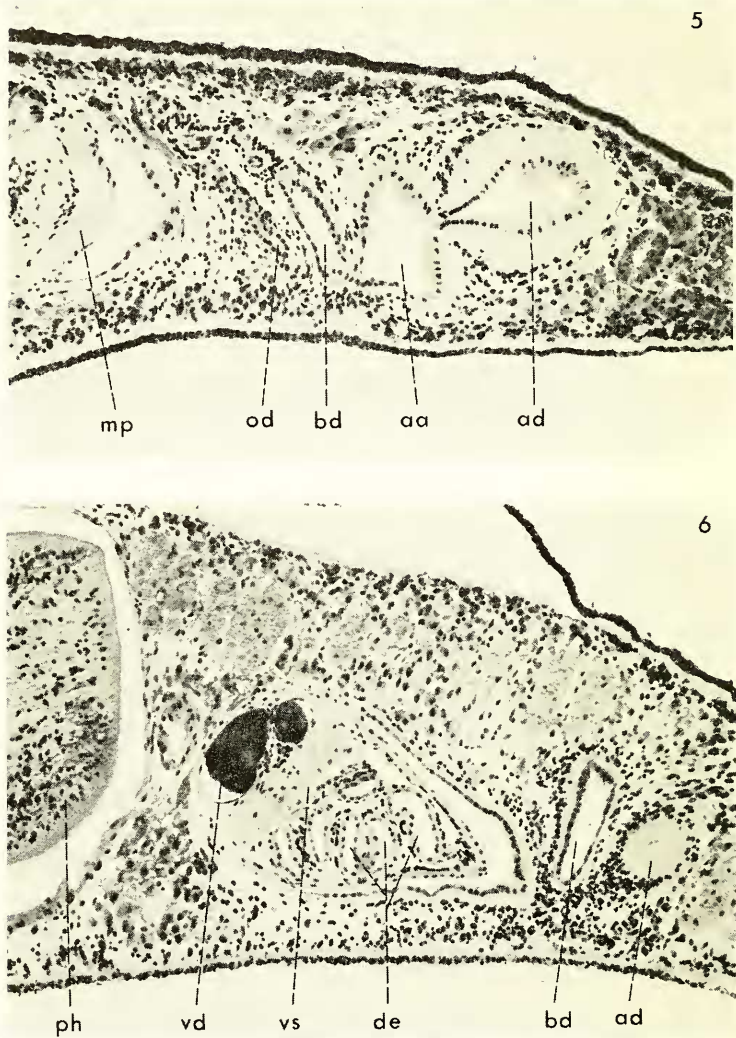


FIG. 5-6. 5. *Planaria dactyligera musculosa*, sagittal section of copulatory complex, showing the adenodactyl (*ad*) with its atrial chamber (*aa*), the terminal part of the bursa duct (*bd*), the thick muscular coat (*mp*) of the penis papilla (excentrically cut), and part of the common oviduct (*od*), $\times 113$. 6. *Planaria occulta*, sagittal section through copulatory complex, showing the position of the pharynx (*ph*), vas deferens (*vd*), seminal vesicle (*vs*), the convoluted ejaculatory duct (*de*), and parts of the bursa duct (*bd*) and adenodactyl (*ad*), $\times 113$.

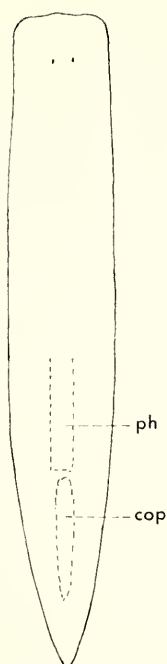


FIG. 7. *Planaria occulta*, outline drawing of gliding animal, *cop*, copulatory complex; *ph*, pharynx.

the substrate by a colorless jelly-like substance, the long axis being parallel to the surface of the substrate (bottom or side wall of the aquarium). They easily loosen their attachment when the cultures are handled. As is the rule in triclad cocoons, the freshly laid egg capsule is of a light reddish-brown color and darkens in a few days to become dark brown to almost black. Three to 14 young hatched from a single cocoon after 3–4 weeks. The freshly hatched young (Fig. 1c) vary in size from 1.5 to 3 mm in length. They are unpigmented, white, with a rounded head end. As they grow in size, they gradually become pigmented and acquire the typical truncate head shape characteristic of older specimens.

No asexual reproduction by fission was observed during 28 months of culturing.

***Planaria occulta* new species[†]**

Type material: Holotype, from Duffield, Scott County, Virginia, 2 slides of sagittal sections, U. S. National Museum No. 39463. Paratypes, sagittal and transversal sections of 7 specimens, in the author's collection.

[†] *occultus*, Latin, hidden, alluding to the subterranean occurrence in a well.

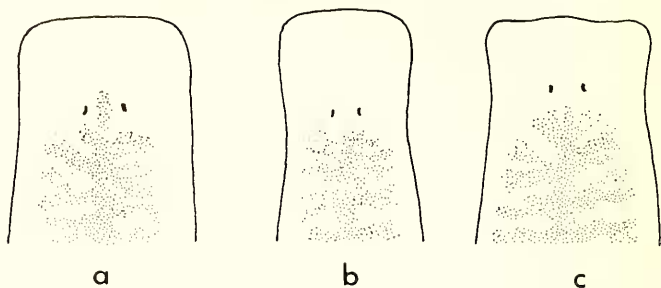


FIG. 8. Anterior ends of three similar planarian species: *a*, *Planaria occulta*; *b*, *Phagocata morgani*; *c*, *Phagocata oregonensis*.

External features (Fig. 3): Mature specimens measure up to 9 mm in length and 1.5 mm in width when gliding quietly. The species is without body pigment, appearing white when the intestine contains no colored matter; even with the intestine filled, the head, the lateral margins of the body, and the places occupied by the pharynx and copulatory apparatus are always white. The head is truncated, with a slightly convex frontal margin and rounded lateral edges (Fig. 8a). In quiet gliding it may transitorily present a moderately bulging median section (Fig. 7). There is no neck constriction behind the head. The lateral margins gradually diverge, soon become parallel, start converging again in the region of the pharynx, and meet at the moderately pointed posterior end. There are two eyes, rather far removed from the frontal margin, their distance from each other amounting to about one-fourth the width of the head at eye level. The distance of each eye from the lateral margin is smaller than that from the frontal margin. No supernumerary eyes, such as frequently occur in normally two-eyed planarians, have been observed in this species. The pharynx is inserted at about the middle of the body and amounts in length to approximately one-fifth the body length. In sexually mature specimens, the copulatory complex occupies the anterior three-fourths of the postpharyngeal region.

At first glance, *Planaria occulta* resembles the common *Phagocata morgani* (Stevens & Boring) with which it shares its geographic area, and other unpigmented species of *Phagocata* of North America (*P. nivca* Kenk, *P. oregonensis* Hyman), Europe, and Japan. Unfortunately not all these species have been adequately described in the living state. In comparing specimens in good physiological condition during gliding locomotion, one may discover subtle differences between these various species, differences which are entirely obscured in the preserved animals. Figure 8 shows such a comparison between *P. occulta* (*a*), *P. morgani* from a spring in Rock Creek Park in Washington, D. C. (*b*), and *P. oregonensis* from Portland, Oregon (*c*). It will be noticed that in *P. occulta* the anterior intestinal ramus ends at a level anterior to the eyes, while in the

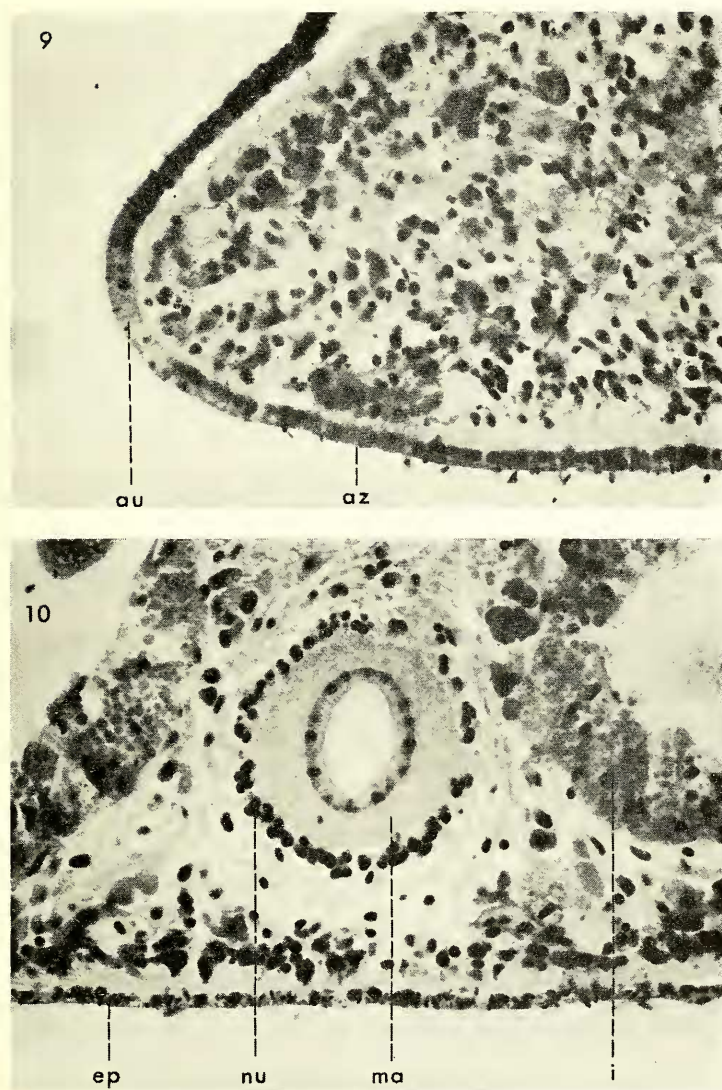


FIG. 9-10. *Planaria occulta*. 9. Paramedian section through the anterior end, showing the auricular sense organ (*au*) and the marginal adhesive zone (*az*), $\times 310$. 10. Cross section of postpharyngeal region at the level of the adenodactyl; *ep*, ventral surface epithelium; *i*, intestinal epithelium; *ma*, muscle layer of adenodactyl; *nu*, layer of muscle cell bodies and nuclei. $\times 310$.

adult *P. morgani* and *P. oregonensis* the intestine is confined to a region posterior to the eyes. It must be mentioned, however, that freshly hatched young of *P. morgani* show an anterior extension of the intestinal ramus between the eyes similar to that of *P. occulta*.

The locomotion of *Planaria occulta* is a smooth gliding. No "crawling" movements such as are observed in many other species have been seen even upon mechanical stimulation of the animal (to which they react by a brief contraction of the body, followed immediately by continued gliding).

Integument: The epithelium of the general surface shows no peculiarities, the cells of the dorsal epithelium being somewhat taller than those of the ventral side (about $12\ \mu$ and $8\ \mu$, respectively, depending somewhat on the contraction of the body). No distinct adhesive organ is developed. A narrow band of gland openings runs ventrally along the margins of the body, the marginal adhesive zone (Figs. 9 & 11, *az*). This band is interrupted only in the center of the frontal margin of the head by a very short ($30\ \mu$ – $35\ \mu$) gap. The secretion of the adhesive glands is granular and strongly cosinophilic.

Sense organs: In addition to the eyes, there are other sensory structures discernible in the head region. The auricular sense organs occupy the lateral parts of the frontal margin and consist of strips of modified epithelium, densely ciliated and containing only few rhabdites which are generally much shorter than those of the surrounding epithelia. There are no sensory pits or grooves developed, as the organs form the very edge of the margin, being separated from the adhesive gland zone by a narrow band of normal surface epithelium. Another sensory area, a small patch with similarly modified rhabdite-free epithelium, lies on the ventral side of the head, immediately behind the gap of the marginal adhesive zone.

Digestive system: The pharyngeal muscles conform with the typical arrangement in the family Planariidae, the muscle fibers of the internal zone forming two separate layers, an inner circular and an outer longitudinal one. The external muscle zone consists likewise of two layers, a layer of longitudinal fibers underlying the outer epithelial covering, followed by a layer of circular fibers. There is no third (longitudinal) layer developed. The anterior intestinal ramus which, as indicated above, extends in the head region to a level in front of the eyes, bears on either side 6 to 9 branches; each posterior ramus, 13 to 19 shorter and less profusely ramified branches.

Reproductive system: The numerous testes occupy a longitudinal zone on either side of the midline, each zone extending from a short distance behind the head to approximately the level of the mouth opening. In a prepharyngeal cross section (Fig. 11) one may see on each side one to six more or less rounded testicular follicles (*t*), situated in the ventral parts of the mesenchyme, mainly below the intestinal branches (*i*) and above the ventral nerve cords (*u*). Individual testicles, particularly at full maturity, may penetrate dorsally in the spaces between the branches of the

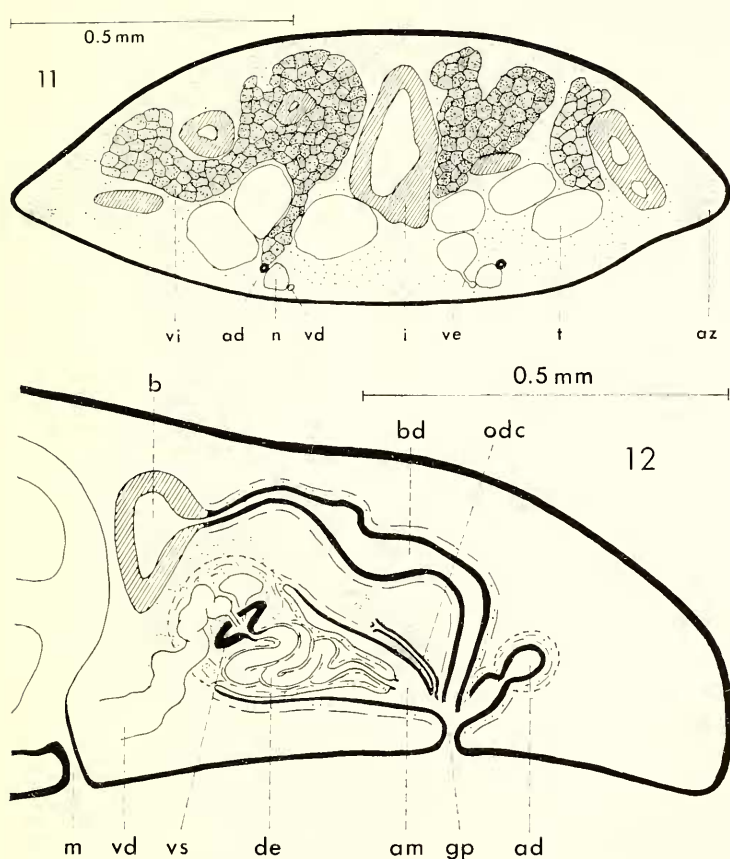


FIG. 11–12. *Planaria occulta*. 11. Transversal section of prepharyngeal region. 12. Semidiagrammatic view of copulatory apparatus in sagittal section. *ad*, adenodactyl; *am*, male atrium; *az*, marginal adhesive zone; *b*, copulatory bursa; *bd*, bursa stalk; *de*, ejaculatory duct; *gp*, gonopore; *i*, intestine; *m*, mouth; *n*, ventral nerve cord; *od*, oviduct; *odc*, common oviduct; *t*, testis; *vd*, vas deferens; *ve*, vas efferens; *vi*, yolk glands; *vs*, seminal vesicle.

intestine. From each testicle a delicate duct, the vas efferens (*ve*), proceeds ventrally to open into the likewise very thin-walled sperm duct or vas deferens (*vd*) of the corresponding side, which runs along the medial border of the ventral nerve cord, close to the subcutaneous muscle layer of the ventral surface. In the region of the pharynx the vasa deferentia expand greatly in diameter and are seen as a pair of tortuous tubes filled

with sperm, the false seminal vesicles (or spermiducal vesicles according to Hyman's [1951: 113] terminology). At the level of the penis they bend upward and enter the bulb portion of the penis from the sides.

The rather small spherical ovaries or germaries are in the typical position, a short distance behind the eyes, adjoining the medial side of the ventral nerve cords. Each ovary is accompanied by more voluminous, lobate masses of cells extending toward the dorsal side, the parovaries. The cytoplasm of these cells stains dark blue with Ehrlich's hematoxylin. The oviducts or ovovitelline ducts start from the lateral surfaces of the ovaries, each beginning with a slightly widened portion, the seminal receptacle. They run caudally along the dorso-lateral side of the ventral nerve cords (Fig. 11, *od*). On their course they connect with numerous yolk glands or vitellaria (*vi*) which, at full maturity, represent voluminous masses occupying chiefly the dorsal and lateral portions of the mesenchyme from the level of the ovaries to almost the posterior end of the body.

The copulatory apparatus (Fig. 12) occupies, in sagittal sections, the greater part of the postpharyngeal region. The genital aperture or gonopore (*gp*) is situated far caudally, its distance from the mouth opening (*m*) being about twice the distance from the tail end of the body. There is no distinctly developed common genital cavity or atrium, as the various ducts of the copulatory complex meet almost at the gonopore: from the anterior side the male atrium (*am*), dorsally the duct of the copulatory bursa (*bd*), and from the caudal side the outlet of a small cavity connected with the adenodactyl (*ad*). The "male" atrium encloses the papilla of the penis and receives in its posterior portion the mouth of the common ovovitelline duct (*odc*). Its lining is an epithelium of cubical, ciliated cells below which are two layers of muscles, a layer of circular fibers and below it one of longitudinal fibers.

The male copulatory organ or penis consists of a moderately developed spherical bulb embedded in the mesenchyme a short distance behind the pharyngeal pouch, and a conical papilla pointing caudally and somewhat toward the ventral side. The bulb consists of a loose arrangement of muscle fibers between which there are very numerous gland ducts containing a fine-grained faintly eosinophilic secretion. These ducts originate from cell bodies lying in the surrounding mesenchyme and open within the bulb into a rather small, usually antero posteriorly compressed cavity, the seminal vesicle (*vs*). Each vas deferens (*vd*), which retains its expanded shape as spermiducal vesicle, enters the penis bulb laterally, forming a few convolutions within the bulb, and finally narrowing to a short canal which opens into the seminal vesicle. At the border between the penis bulb and the penis papilla the seminal vesicle connects with the ejaculatory duct (*de*). This is, in its main portion, a highly convoluted tube of about even diameter. Only its terminal part gradually narrows and straightens out in the axis of the papilla, to open to the outside at its tip. This opening is encircled by a small collarlike projection of the papilla. The space between the outer wall of the papilla and the

convolutions of the ejaculatory duct contains a very loose parenchyma, often giving the impression of an empty space. This condition, as well as the fact that the ejaculatory duct does not have the typical shape of a straight tube makes it possible to speculate whether the ejaculatory duct is not capable of evagination (like the cirrus of trematodes and cestodes, or the proboscis of nemerteans). Evidence of a partial eversion was seen in at least one of the eight specimens sectioned.

The epithelium lining the seminal vesicle consists of columnar to cubical cells perforated by the numerous gland ducts which have penetrated the penis bulb from the outer mesenchyme. The lining of the ejaculatory duct is a cubical, the outer covering of the penis papilla a flattened epithelium. Both epithelia have associated muscular layers: circular and longitudinal fibers on the papilla and chiefly longitudinal fibers on the ejaculatory duct.

The copulatory bursa (*b*) is a more or less rounded sac situated in the mesenchyme immediately behind the pharyngeal pouch, lined with a rather tall glandular epithelium. Its duct or stalk (*bd*) proceeds from its dorso caudal side posteriorly as a rather narrow canal, then gradually widens forming some convolutions above the atrium, and, after narrowing slightly, bends ventrally and opens into the atrial complex close to the gonopore. There is, therefore, no enlarged terminal section or vagina present. The duct is lined with a cubical epithelium which bears cilia at least in the distal (posterior) part of the canal. It is surrounded by a well-developed muscle coat of circular fibers adjoining the epithelium, followed by a layer of longitudinal fibers.

The two oovitelline ducts, which accompany the ventral nerve cords in the anterior part of the body, deviate from their course at the level of the penis, ascend dorsally along the wall of the male atrium and unite in the space between atrium and bursa stalk. The common oviduct (*od*) thus formed runs postero ventrally along the roof of the atrium and opens, without further differentiations, into the posterior portion of the atrium. The paired oviducts from the place where they are separated from the nerve cords, and the entire unpaired or common oviduct receive many gland ducts with an intensively eosinophilic secretion from the surrounding mesenchyme. These glands are generally termed "shell glands" although their function is doubtful and probably has nothing to do with the formation of the shell of the cocoon.

The adenodactyl (*ad*) is a very distinct ellipsoidal or almost spherical hollow organ situated near the ventral side a short distance posterior to the gonopore. It consists mainly of a highly muscular covering enclosing a round cavity. The muscle fibers of the organ are very densely arranged, mainly in a circular direction, with their cell bodies and nuclei forming a distinct peripheral layer (Fig. 10, *nu*). Gland ducts seem to penetrate the muscular coat from the outer mesenchyme, but do not show up clearly after staining with hematoxylin and eosin. The lumen of the adenodactyl opens into a small compartment of the genital atrium which extends posteriorly from the vicinity of the gonopore. There may be a small papilla

protruding from the adenodactyl into this compartment, or this papilla may be entirely absent, depending on the state of contraction of the copulatory complex. The cavity of the adenodactyl is lined with a cubical ciliated epithelium. In the sections examined, the cavity was usually empty, without an accumulation of secretions.

Distribution: *Planaria occulta* has so far been found in only one locality, a hand-dug well, about 4 m deep, just east of the town of Duffield, Scott County, Virginia, on the property of Mr. Corbett Brown. The first specimens brought to my attention were collected by Dr. John R. Holsinger and Mr. Sam Pinkerton on 11 March 1967. They were preserved in formalin and showed the reproductive system well developed. A second lot of sexually mature specimens, collected 8 April 1967 by Dr. Holsinger, were received in the living state. On 26 November 1968 I visited the locality, submerged some liver bait in the well, and collected next morning about 100 specimens of various sizes, the majority having developed reproductive structures. The water temperature at that time was 11.8°C.

Ecology: It is difficult to decide whether the hypogean occurrence of the species is obligate, as the surface waters of the geographic area have not been examined systematically. The fact that sexually mature animals were collected in March, April, and November makes it probable that their sexual maturity is not of a seasonal nature. In the laboratory the animals kept very well in spring water cultures at 14°C and accepted beef liver and *Tubifex* worms as food. However, no egg capsules were deposited during five months of culturing, nor was there any evidence of asexual reproduction by fission.

Taxonomic position: The general arrangement of the various parts of the copulatory apparatus and the presence of a hollow adenodactyl place the species in the genus *Planaria*. While the remaining species of this genus *P. torva*, *P. kempfi*, and *P. dactyligera*, form a closely related group with many characteristics in common, the new species occupies a somewhat isolated position. Apart from the lack of body pigment (which is also occasionally seen in *P. torva*, see Reisinger [1963: 685], and in the cavernicolous subspecies *P. torva stygia* Kenk [1936: 7]), some features of the copulatory apparatus deviate considerably from the conditions seen in the type-species of the genus. Among these, the most outstanding difference concerns the anatomy of the penis: the presence of a sinuous, probably eversible ejaculatory duct. The adenodactyl likewise differs in some details from that of *P. torva*.

Parasites: All specimens of *Planaria occulta* sectioned or investigated in squash preparations were heavily infested with the holotrichous ciliate *Sieboldiellina planariarum* (Siebold), a parasite commonly found in *P. torva* (see Meixner, 1928: 604, etc.) and other freshwater triclads. The ciliates were always found in the rami and branches of the intestine, less often in the pharyngeal pouch, and occasionally in the copulatory bursa. This latter observation supports the interpretation maintained chiefly by Steinböck (1966: 167, etc.) that the bursa is a derivative of

the intestine which has retained many of the functions of that organ as well as part of its chemical environment.

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